

Convergent evolution of morphology and habitat use in the explosive Hawaiian fancy case caterpillar radiation

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Abstract

Species occurring in unconnected, but similar habitats and under similar selection pressures often display strikingly comparable morphology, behaviour and life history. On island archipelagos where colonizations and extinctions are common, it is often difficult to separate whether similar traits are a result of *in situ* diversification or independent colonization without a phylogeny. Here, we use one of Hawaii's most ecologically diverse and explosive endemic species radiations, the Hawaiian fancy case caterpillar genus *Hyposmocoma*, to test whether *in situ* diversification resulted in convergence. Specifically, we examine whether similar species utilizing similar microhabitats independently developed largely congruent larval case phenotypes in lineages that are in comparable, but isolated environments. Larvae of these moths are found on all Hawaiian Islands and are characterized by an extraordinary array of ecomorphs and larval case morphology. We focus on the 'purse cases', a group that is largely specialized for living within rotting wood. Purse cases were considered a monophyletic group, because morphological, behavioural and ecological traits appeared to be shared among all members. We constructed a phylogeny based on nuclear and mitochondrial DNA sequences from 38 *Hyposmocoma* species, including all 14 purse case species and 24 of non-purse case congeners. Divergence time estimation suggests that purse case lineages evolved independently within dead wood and developed nearly identical case morphology twice: once on the distant Northwest Hawaiian Islands between 15.5 and 9 Ma and once on the younger main Hawaiian Islands around 3.0 Ma. Multiple ecomorphs are usually found on each island, and the ancestral ecomorph of *Hyposmocoma* appears to have lived on tree bark. Unlike most endemic Hawaiian radiations that follow a clear stepwise progression of colonization, purse case *Hyposmocoma* do not follow a pattern of colonization from older to younger island. We postulate that the diversity of microhabitats and selection from parasitism/predation from endemic predators may have shaped case architecture in this extraordinary endemic radiation of Hawaiian insects.

Introduction

Natural selection serves as one of the fundamental mechanisms in the speciation process (Darwin, 1859). Organisms that share comparable habitats often appear

alike because of similar selection pressures that acted prior to their diversification, or because of convergent selection acting on unrelated lineages (Losos *et al.*, 1998; Blackledge & Gillespie, 2004; Emerson & Gillespie, 2008; Cavender-Bares *et al.*, 2009). On island archipelagos where colonizations and extinctions are common (MacArthur & Wilson, 1967), it is often difficult to separate whether similar traits are a result of *in situ* (within archipelago) diversification from a single ancestor by unrelated lineages that have independently

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colonized and faced similar selection pressures from the insular environment. A phylogenetic analysis that samples a suite of species and traits across the archipelago allows one to test whether similar traits evolved due to diversification or by convergence.

The importance of founder events in initiating species diversification has been extensively studied both theoretically and empirically on islands (e.g. Gillespie & Roderick, 2002; Losos & Ricklefs, 2009). Organisms that colonize new islands are typically faced with low inter-specific competition, empty niche space and lack of predators or parasitoids (Whittaker & Fernández-Palacios, 2007; Santos *et al.*, 2011). The availability of similar ecological niches on different islands can often lead to similar phenotypes in unrelated lineages. *Anolis* lizards, a textbook example of an adaptive radiation on islands, fill in similar ecological niches on multiple Caribbean islands, and this has led to habitat specialists that utilize different areas of a plant (Losos *et al.*, 1998; Losos, 2009). A similar phenomenon is seen among land snails of the Bonin Islands (Chiba, 2004) and orb-weaving spiders in Hawaii (Gillespie *et al.*, 1997; Blackledge & Gillespie, 2004), where these organisms have filled similar ecological niches on multiple islands and are characterized by similar morphological features. In some cases, the sequence of these 'ecomorphs' can be stepwise and predictable, where certain traits have repeatedly evolved from others (Losos, 1992).

Due to their high peaks, deep valleys, rainfall gradients and microhabitat diversity, the Hawaiian archipelago is a model system to test whether similar environments have led to convergent traits. Hawaii is one of the most isolated archipelagos in the world with an array of different climate zones and ecosystems (Carson & Clague, 1995). The biota is almost entirely derived *in situ*, making it an exceptional laboratory to study the effect of habitat similarity on the speciation process. The archipelago's sequential series of island ages provides an ideal test system because each Hawaiian island can be dated chronologically and thus serves as an important timeline to estimate when morphological and behavioural changes took place (Funk & Wagner, 1995).

With more than 350 species inhabiting a vast array of ecological niches and displaying incredible variability in larval case architecture, the endemic Hawaiian moth genus *Hypsmocoma* is a spectacular example of an insular radiation (Zimmerman, 1978; Schmitz & Rubinoff, 2011a) and an ideal group on which to test the effects of microhabitat use on phenotypic variation. Unlike the larvae of most moths and butterflies, *Hypsmocoma* caterpillars construct portable silk cases in which they reside. A diversity of larval case architectures exists, and each case type is thought to represent a monophyletic evolutionary lineage, usually composed of allopatric species (Rubinoff & Schmitz, 2010). The spectacular, unusual and varied architecture of the cases has inspired nicknames like burritos, bugles, candy wrappers,

cones and purses (Rubinoff & Schmitz, 2010; Schmitz & Rubinoff, 2011a).

Purse case making species construct a long, smooth, brown silk case, with a centralized white spot from which circular rings radiate (Schmitz & Rubinoff, 2009; Kawahara & Rubinoff, 2012) (Fig. 1a,b). At least fourteen species of *Hypsmocoma* are purse-case makers (Kawahara & Rubinoff, 2012), and each is believed to be endemic to a single island. They are found on all five of the main islands and at least two of the Northwest Hawaiian Islands (NWHI) (Rubinoff & Schmitz, 2010; Kawahara & Rubinoff, 2012). Purse case larvae prefer damp microhabitats, such as deep within tree fern fronds or rotting wood where the larvae eat soft dead plant tissue (Kawahara & Rubinoff, 2012). Purse case *Hypsmocoma* are part of a group of species within *Hypsmocoma* whose caterpillars make dual-entry cases, allowing the larva to enter or exit from either end. At pupation, larvae thread their cases closed on each end and fasten them to the substrate. Because of these behavioural, ecological and morphological traits, purse case species have traditionally been grouped together and were thought to represent a single evolutionary origin (Zimmerman, 1978; Kawahara & Rubinoff, 2012).

Although purse case *Hypsmocoma* are widespread across the Hawaiian archipelago, no work on their evolutionary ecology has been conducted because the group is challenging to collect and difficult to rear in captivity. Their diversity and apparent monophyly provide an ideal lineage for biogeographic analysis and an associated molecular clock-based dating of divergence times. Such an analysis contributes directly to a growing body of knowledge about the pace and pattern of species divergence across the Hawaiian Islands (e.g. O'Grady & Desalle, 2008; Garb & Gillespie, 2009; Hayes *et al.*, 2009; Goodman *et al.*, 2012; Rubinoff *et al.*, 2012).

We present a multigene phylogeny of *Hypsmocoma* that includes representatives of all major lineages. We also test whether *in situ* diversification has led to similar case architecture in comparable habitats by applying a Bayesian relaxed clock with geologic calibrations to islands to infer the age of *Hypsmocoma*. We investigate the systematic position of purse case *Hypsmocoma*, evaluating its monophyly and biogeography, and discuss the implications of our results in the larger context of both *Hypsmocoma* larval case evolution and Hawaiian biogeography.

Materials and methods

Taxon sampling, amplification and sequencing

We sampled 70 *Hypsmocoma* from 38 species, representing all known morphological, ecological and behavioural lineages in the genus as previously defined

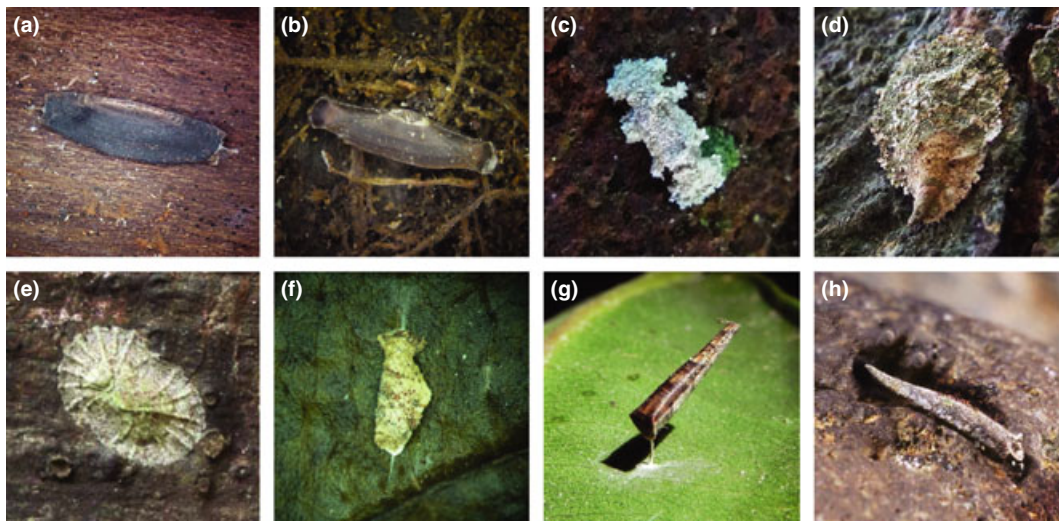


Fig. 1 Comparisons of *Hypsocoma* larval cases. (a) *Hypsocoma filicivora*, purse case, Oahu; (b) *Hypsocoma auropurpurea*, purse case, Oahu; (c) *Hypsocoma wahikanake*, candy-wrapper case, Lanai; (d) *Hypsocoma* sp., oyster case, Molokai; (e) *Hypsocoma* sp., modified candy-wrapper case, Kauai; (f) *Hypsocoma* sp., burrito case, Kauai; (g) *Hypsocoma* sp., bugle case, Hawaii; (h) *Hypsocoma kamakou*, cone case, Molokai.

(Zimmerman, 1978; Rubinoff & Schmitz, 2010; Schmitz & Rubinoff, 2011a). We included *Labdia issikii* and *Limnaecia* sp., cosmopterigids that are morphologically closely related to *Hypsocoma* (Zimmerman, 1978) as outgroups, along with two species of *Euperissus*, the presumed Hawaiian sister group to *Hypsocoma*.

Three independent loci, comprising 2238 bp of DNA, were sequenced for phylogenetic analysis. These included two nuclear genes: the *Carbamoylphosphate Synthase* domain of CAD (CAD; 705 bp), *Elongation factor 1-alpha* (EF-1 α ; 771 bp), and the mitochondrial gene *Cytochrome c Oxidase I* (COI; 762 bp). Extraction, amplification and sequencing procedures for these genes largely follow our previous work (Rubinoff & Schmitz, 2010; Schmitz & Rubinoff, 2011b; Kawahara & Rubinoff, 2012; Rubinoff *et al.*, 2012). Sequencing was conducted at the Greenwood Molecular Biology Facility, Pacific Biosciences Research Center, University of Hawaii at Manoa (www.pbrc.hawaii.edu/gmbf).

For each sample, both sense and antisense strands of the PCR products were sequenced. Contigs were assembled into complete sequences with the software program GENEIOUS 5.4 (Drummond *et al.*, 2011). Nucleotide positions that could not be determined with certainty were edited with the appropriate IUPAC ambiguity code. Sequences were aligned using the 'Geneious alignment' option (65% similarity cost matrix, gap open penalty = 12, gap extension penalty = 3, refinement iterations = 2). Supplementary Table S1 lists all sequences, code names and GenBank accession numbers. The concatenated data set is available from the Dryad data depository (<http://datadryad.org>).

Phylogenetic analysis

Two model-based methods were used to estimate phylogenetic relationships: maximum likelihood (ML) and Bayesian inference. Our methods largely follow previously published approaches (e.g. Kawahara *et al.*, 2009; Regier *et al.*, 2009; Scott *et al.*, 2010; Cho *et al.*, 2011; Kawahara & Rubinoff, 2012; Rubinoff *et al.*, 2012) with some modifications. Maximum likelihood analyses were implemented in RAXML 7.3.2.0705 (Stamatakis, 2006). We used PARTITIONFINDER 1.0.1 (Lanfear *et al.*, 2012) to determine the best substitution model for nine different partitions; a partition was assigned to each codon position of the three genes. One thousand ML and one thousand bootstrap tree searches were conducted as implemented in RAXML. Bayesian analyses were conducted with MRBAYES 3.2.1 (Ronquist & Huelsenbeck, 2003) with the appropriate substitution model for each partition and run for 25 million generations, sampling every 1000th tree. Chain convergence was evaluated with MRBAYES. All phylogenetic analyses were initially conducted for single genes as an error-checking measure and to assess phylogenetic congruence. Tree searching strategies for the all-gene concatenated data set were the same as those for individual loci. We also examined data sets that excluded third positions ('nt12') and disregarded synonymous changes ('dgen1' Regier *et al.*, 2010), the latter of which eliminates the contribution of any synonymous change to pairwise differences between taxa, which may reduce homoplasy in molecular data sets.

Hypothesis testing

The Approximately Unbiased (AU) test of Shimodaira (2002) was implemented to (1) compare confidence between our results and a prior morphology-based hypothesis that purse cases are monophyletic and to (2) test whether a single origin of dual-entry *Hypsmocoma* cases can be statistically rejected. We conducted two separate ML analyses that constrained the monophyly of the two groups. The AU statistical test was conducted in CONSEL 0.20 (Shimodaira & Hasegawa, 2001) to determine the difference in fit to data of the constrained and unconstrained trees, using scripts that were developed in previous studies (Regier *et al.*, 2009; Cho *et al.*, 2011; Kawahara *et al.*, 2011a). We also conducted a Bayesian topological test (Huelsenbeck *et al.*, 2002) to examine the number of trees in the posterior distribution of the MCMC chains that had a topology that fit the constraint.

Ecomorphs and larval case architecture

The microhabitat type of each species was identified through extensive fieldwork. Fancy case caterpillars were collected between 2003 and 2011 from nearly all Hawaiian Islands and reared in the laboratory at the University of Hawaii at Manoa. Larval cases were assigned separate petri dishes, all cases were digitally imaged with a Ricoh CX5 camera, and the locality and microhabitat from which the case was collected was recorded and databased. Each case type was identified based on case architecture, such as axes of symmetry, presence of flanges and ornamentation. Additional details on *Hypsmocoma* rearing methods can be found in the study by Schmitz & Rubinoff (2011a,b). Each species was scored into the following ecomorphs depending on the microhabitat that they utilized: (1) dry exposed rocks, (2) rocks within streams, (3) tree bark, (4) leaf surfaces, (5) dead wood and (6) leaf litter. Case types followed the definitions of Schmitz & Rubinoff (2008), Schmitz & Rubinoff (2009, 2011a,b). These included (1) cone, (2) burrito, (3) bugle, (4) oyster, (5) candy wrapper, (6) snail eater, (7) purse and (8) lignivora. The 'abjecta' case form was previously undescribed but represents a case type that differs from others (Kawahara unpublished data).

Ancestral state reconstruction of ecomorphs was conducted in RASP v. 2.0 (Yu *et al.*, 2011), a program that uses a Bayesian ancestral state reconstruction method and calculates the probability of each habitat type on each node, averaged over all sampled trees. We used the 10 000 trees sampled from the posterior distribution of the MrBayes analysis and plotted frequencies of the six microhabitats on the ML topology. We ran 10 chains for 5×10^6 generations in RASP, sampling every 1000 generations with a burnin of 2×10^6 with the outgroup option set to wide.

Divergence time estimation

No fossils for *Hypsmocoma* are known, but because the Hawaiian archipelago is a volcanic island chain with a linear, chronological progression of island formation, we assigned calibrations to internal nodes that correspond to the geologic ages for the emergence of different islands. We applied age estimates of three Hawaiian islands from widely accepted estimates proposed by Price & Clague (2002) to 'candy wrapper' and 'cone' case clades that are known to follow the progression rule (Rubinoff & Schmitz, 2010; Schmitz & Rubinoff, 2011b). The 'progression rule' posits that species found on older islands are basal to those from younger islands, thus resulting in a sequence of colonizations that correspond to island ages in groups that follow the rule (Funk & Wagner, 1995). The three calibrations, corresponding to numbered nodes in Fig. 2, are: (1) 4.7 Ma, split between NWHI and Kauai; (2) 3.0 Ma, split between Kauai and Oahu; and (3) 2.2 Ma, split between Oahu and Maui-Nui. Because there are uncertainties in true island ages, we assigned a conservative 95% confidence interval that extends to $\pm 30\%$ the mean island age.

To estimate divergence times, we used an uncorrelated lognormal clock as implemented in BEAST 1.7.2 (Drummond & Rambaut, 2007). BEAST analyses were run with a Yule process for model of speciation, with a diffuse gamma prior (shape 0.001, scale 1000) assigned to the ucln mean. The gamma prior was changed because the default setting prevented chain convergence. The expected mean Yule Birth Rate (YBR) was calculated based on the formula $(\log [N/2])/T$, where $N = 28.7$ Ma and $T = 70$. The rate is based on total tree depth in units of time (T) and the number of terminals in the data set (N). The maximum tree depth was based on Price & Clague's (2002) estimate of the age of Midway Atoll, the oldest island on which *Hypsmocoma* is recorded (Nishida & Beardsley, 2002). This approach was taken because the YBR prior in BEAST 1.7 is set at an unrealistic flat (i.e. uniform) prior by default. Although a flat YBR prior may seem appropriate, true uniform priors that extend to infinity do not exist in nature, which ultimately can bias the prior to a fast birth rate and can lead to unrealistically recent estimates. All phylogenetic analyses and divergence time estimation analyses were conducted on the University of Florida High Performance Computing (HPC) Cluster (www.hpc.ufl.edu/).

Results

Sequencing and phylogenetic relationships

We obtained nearly 2.4 kb of nuclear and mitochondrial sequence data from 70 specimens identified as *Hypsmocoma* or outgroups in the cosmopterigid genera,

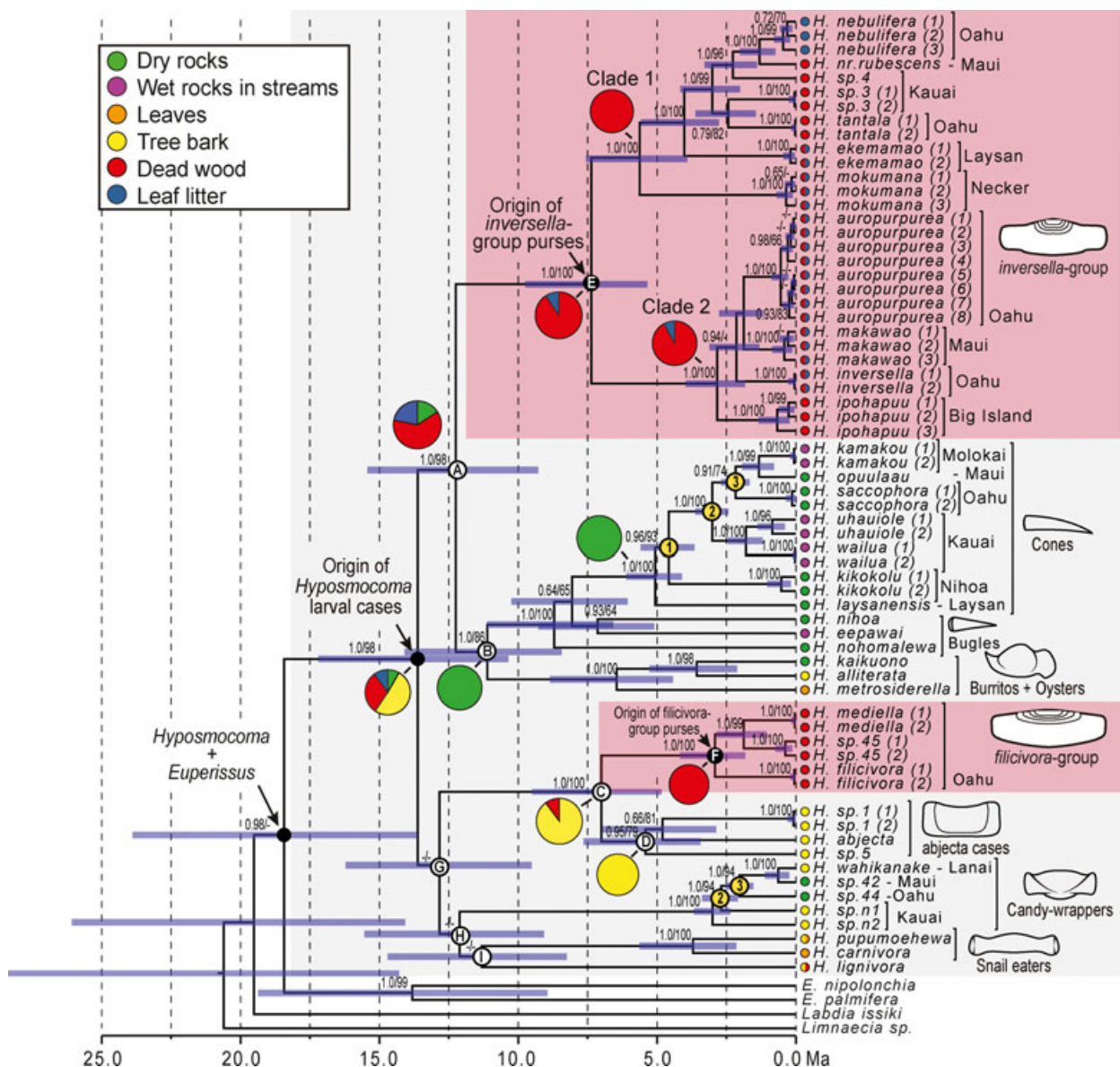


Fig. 2 Bayesian consensus of *Hypsoscoma* showing 95% confidence intervals of posteriors as calculated in BEAST. Numbers above branches are Bayesian (MrBayes) posterior probabilities (PP) and ML bootstrap values (BP), respectively. Node numbers indicate the five calibration points: 1 = 4.7 Ma, 2 = 3.0 Ma, 3 = 2.2 Ma. Nodes A through I refer to clades that are discussed in the text. Coloured circles indicate microhabitat types and ancestral state probabilities.

Euperissus, *Labdia* and *Limnaecia*. Sequences for some samples did not amplify, but the amount of missing data in the concatenated data set of all genes was relatively small (10.6%). There was little evidence of conflicting signal from different loci, as each gene tree provided largely congruent topologies with the tree based on the concatenation of all genes, in both an ML and Bayesian framework. Slight differences were found in the branching pattern within *H. aurorepurea*, but bootstrap support for these differences was never above 50%. Analyses that included only the first and second

codon positions (nt12) and only slower-evolving non-synonymous changes (degen1) yielded virtually no informative phylogenetic signal for this study, suggesting that most of the phylogenetic signal was coming from synonymous substitutions at nt3. Indeed, 91.5% of third positions were variable, whereas nt1 and nt2 were only 59.9% and 48.6% variable. The ML tree (lnL = -14758.462646) and MrBayes consensus from the concatenated data set were identical in topology. MrBayes analyses were terminated at 25 million generations, and the average split frequencies between the

two chains fell below 0.01 at 600 000 generations. Ten thousand trees from each MCMC chain were sampled from the posterior distribution.

Purse case species were split into two distinct clades: the *H. filicivora* group of three species and the *H. inversella* group of 12 species. Branch support for these two groups was high [1.0 Bayesian posterior probability (PP) and 100% ML bootstrap (BP) for both; Fig. 2]. There was strong support (1.0 PP, 98 BP) for a sister group relationship between the *inversella* group and Clade B (1.0 PP, 86 BP), which includes bugle, burrito, cone and oyster case species. The sister group of the *filicivora* group constituted *H. abjecta* and two undescribed species (0.95 PP, 79 BP, Node D, Fig. 2).

Within the *filicivora* species group, three well-supported independent lineages occur on the island of Oahu: *H. filicivora*, *H. mediella* and the undescribed '*Hyposmocoma* sp. 45' which was sequenced by Rubinoff & Schmitz (2010). The *inversella*-clade purses also form two well-supported clades: one that includes two Northwest Hawaiian island species, *H. mokumana*, from Necker and *H. ekemamao* from Laysan, as the two most basal lineages (Clade 1). The *inversella* clade also includes *H. ipohapuu* from the island of Hawaii (Big Island), *H. inversella* from Oahu and the more derived *H. auropurpurea* and *H. makawao* from Oahu and Maui (Clade 2).

Hypothesis testing

A prior morphology-based study suggested that purse case species constitute a monophyletic group (Zimmerman, 1978). The ML constraint analysis that tested this hypothesis resulted in a tree ($\ln L = -14688.773796$) that was statistically rejected by the AU test ($P < 0.0001$). The Bayesian topological test resulted in no trees that had a topology fitting the constraint. The ML tree from the constraint analysis that tested the monophyly of dual-entry cases (Hypothesis 2) had a lower likelihood ($\ln L = -14696.422409$) than the unconstrained tree, but this hypothesis was not rejected (AU test, $P = 0.185$). Only eight of 20,000 sampled trees (0.0004%) were found to fit the constraint topology in the MrBayes posterior distribution.

Ancestral state reconstruction of ecomorphs

Purse case specimens were nearly always collected from concealed microhabitats, such as within rotting wood or in dead tree fern stems. This ecological strategy is distinct from burrito case species which were found only on dry tree bark and rocks; bugle and snail-eater cases that were sampled from exposed leaves and bark; candy wrapper, *abjecta* and oyster cases that were localized to surfaces of tree bark; and cone cases that were collected on rocks near or within streams. Ancestral state reconstruction revealed that the ancestors of

the *inversella* and *filicivora* purse cases independently invaded dead wood and evolved nearly identical case morphologies. The dead wood ecomorph was recovered as the ancestor of the *inversella* group with a 90% probability (Node E), and the same was recovered with a $> 99\%$ probability for the ancestor of the *filicivora* group (Node F, Fig. 2). Whereas additional taxon sampling is clearly necessary, our initial results suggest that the ancestor of *Hyposmocoma* might have been associated with tree bark (Fig. 2).

Divergence time estimation

The two parallel BEAST analyses were run for 75 million generations, and a total of 15,000 trees were sampled from the posterior distribution of each chain. Divergence time estimation analyses suggest that the *filicivora* species group shares a most recent common ancestor with their closest relative, the *abjecta*-group, at a maximum age of approximately 7.0 Ma (Node C, Fig. 2), before the emergence of Oahu (3.0–2.6 Ma). Purse case species in the *inversella* group appear to have a shared origin around 7.4 Ma, which roughly coincides with the age of the North West Hawaiian Island of Nihoa (Price & Clague, 2002). The tree obtained from the BEAST analysis (Fig. 2) was nearly identical in topology to the ML tree and MrBayes consensus, only differing in the position of the snail-eating lineage. The snail eaters are grouped with the candy wrappers in the BEAST analysis, but were placed as a sister group to 'Clade A' in the ML tree and MrBayes consensus, though with low support (< 0.5 PP; < 50 BP).

Discussion

In situ convergent evolution of larval cases in Hawaii

Our molecular phylogeny of *Hyposmocoma* reveals a fascinating example of *in situ* convergent evolution in moths that utilize the same microhabitat and acquired nearly identical case architectures on different islands, millions of years apart. Species that construct purse cases appear to have independently evolved to survive within rotting wood, first around 7.4 Ma on the now partially submerged NWHI and subsequently 3.0 Ma on the island of Oahu. There was strong support grouping each purse case type with a non-purse case clade, and trees constructed under the assumption that purse case species had a single evolutionary origin were statistically rejected. This result bears on the repeatability of evolution because the purse case is particular and distinct from all other case types. To have it evolved twice, in independent groups within *Hyposmocoma*, when a myriad of other case morphologies are present and theoretically possible solutions, indicates a predisposition towards a similar evolutionary outcome in the same microhabitat.

Our results are fairly consistent with a previous study on the morphology of land snail shells on islands. Chiba (2004) examined how shell morphology correlates with the microhabitat and islands that they inhabit. Shells of species that occupy different microhabitats differ markedly, but shells of species with the same ecomorph are very similar to each other. In certain instances, shell morphologies of phylogenetically distantly related species that share the ecomorph were indistinguishable.

Whereas taxa in the two purse case groups share a distinctive, smooth, hard case and behavioural and ecological similarities, we discovered that there are small differences in the structure of their cases. For instance, the cases of the *filicivora* group have a simple thin slit at either end of the case as an entry, and the entrance of the *inversella*-group case is slightly rounded and can be closed behind the larva after it retreats into its case (Fig. 3). The slightly rounded case of the *inversella* group is probably associated with a transition from internal wood tunnelling to foraging in leaf litter (red and blue circles; Fig. 2). Minor differences in largely congruent phenotypes are fairly common (McGhee, 2011), as they have also been found in distantly related groups, such as Hawaiian songbirds (Fleischer *et al.*, 2008), tropical butterflies (Endler, 1981) and cichlid fishes (Kocher *et al.*, 1993). These results suggest that although there are cases of indistinguishable morphological convergence (e.g. Chiba, 2004; Muschick *et al.*, 2012), such instances of near-perfect convergence are rare. Convergent evolution in invertebrates is now widely viewed as more common than previously thought (Moore & Willmer, 1997; Breinholt *et al.*, 2012).

It is important to emphasize that our analyses, especially the divergence time estimation analyses, include

inferences that are subject to several sources of error. First, incorrect calibration points can lead to misleading age estimates for other nodes (e.g. Doyle & Donoghue, 1993; Magallón & Sanderson, 2001; Roger & Hug, 2006; Ware *et al.*, 2010). Second, the density of taxon sampling is important for an accurate reconstruction of divergence time estimation (e.g. Linder *et al.*, 2005). Although we included 42 *Hypsimocoma* species from all species groups, they comprise only about 12% of known species in this genus. Many *Hypsimocoma* species are rare and possibly extinct, making complete taxon sampling a challenging task. In general, our data resolved *Hypsimocoma* into well-supported clades, each associated with a particular case type, but support between different case types was in some instances weak (e.g. Nodes G-I, Fig. 2). Additional characters may improve this aspect of the phylogeny; alternatively, it could reflect a rapid radiation that may remain unresolved even with further data.

Biogeography and the progression rule

Hypsimocoma appears to have evolved approximately 17–10.5 Ma, but our phylogeny does not provide clear evidence for the origin of *Hypsimocoma*'s ancestor. This uncertainty is largely due to the fact that few cosmopterigid outgroups have been sampled across the Pacific Rim. Our dates for the origin of *Hypsimocoma* are more recent than another major endemic Hawaiian radiation, *Drosophila*, which is thought to have diversified on the Hawaiian Islands approximately 32 Ma (Russo *et al.*, 1995).

The 'progression rule' pattern of colonization often characterizes many endemic Hawaiian lineages (e.g. Funk & Wagner, 1995; Roderick & Gillespie, 1998; Holland & Hadfield, 2004; Rubinoff, 2008), but our analyses of purse case *Hypsimocoma* did not result in a clear chronological branching pattern of colonization. For instance, 'Clade 1' in the *inversella*-type purses appears to have first occupied the NWHI, but subsequently 'back dispersed' up the chain to the older Laysan Atoll (Fig. 4). We base this conclusion on the fact that a younger island (Necker) has a more basal species (*H. mokumana*) than the derived *H. ekemamao* from Laysan.

Another exception to the progression rule is found in 'Clade 2' (Fig. 4), where the basal species in this clade is *H. ipohapuu* from the youngest island of Hawaii, and the other taxa are from Maui and Oahu. A similar pattern, where the most basal group is from the youngest Hawaiian island, has been reported in bees (Magnacca & Danforth, 2006), cave-dwelling moths (Medeiros *et al.*, 2009), damselflies (Jordan *et al.*, 2003), geese (Paxinos *et al.*, 2002) and land snails (Holland & Cowie, 2007), suggesting that colonization patterns that do not follow the progression rule may be common among endemic Hawaiian lineages.

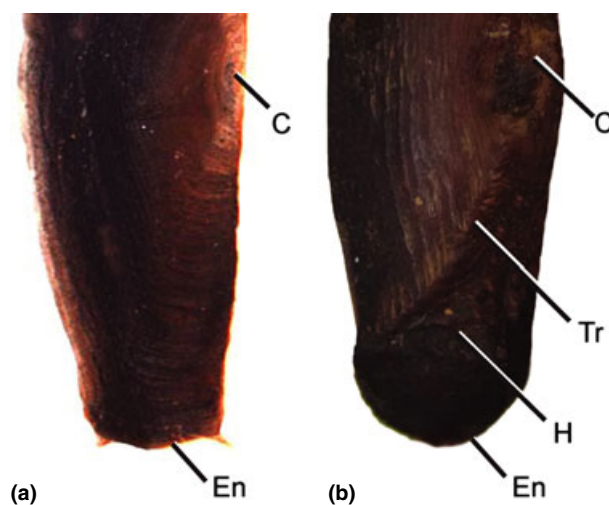


Fig. 3 Two different purse case types. (a) *Hypsimocoma filicivora*. (b) *Hypsimocoma inversella*. (c) crown; En, entrance; H, hood of entrance; Tr, transverse ridge.

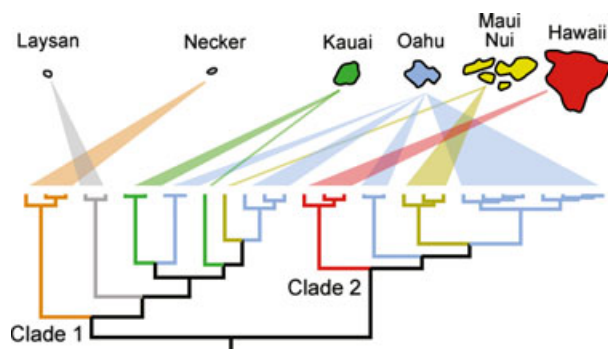


Fig. 4 Relationships of *invesella*-group purses and their colonization pattern on the Hawaiian islands. The *invesella*-group purses do not follow a clear progression rule. Clade 1 and 2 refer to the same clades as in Fig. 2.

We predict that purse case *Hyposmocoma* are not following a progressive colonization pattern because of their ability to disperse. Small moths are often blown across large distances and can colonize remote islands (Smithers, 1977; Hembry *et al.*, 2012), and their dispersal can be heavily dependent on wind currents (Shaw & Hurst, 1969; Chapman *et al.*, 2002). Wind currents vary dramatically in different seasons in Hawaii, which could lead to back-dispersal to older islands from younger ones. Although studies on colonization patterns of small moths on isolated islands are limited, our result is consistent with the microlepidopteran genus *Galagete* in the Galapagos, which also displays a pattern of colonization and speciation that does not follow the geological formation of the islands, but rather a stochastic colonization scenario (Schmitz *et al.*, 2007).

Microhabitats and the evolution of purse cases

Following a colonization event, several ecological processes take place, including density compensation, ecological release, niche expansion and niche shifts (Gillespie & Roderick, 2002; Losos & Ricklefs, 2009; Parent & Crespi, 2009; Yoder *et al.*, 2010), which are enhanced by low interspecific competition, empty or niche space, and lack of predators or parasitoids (Whittaker & Fernández-Palacios, 2007; Santos *et al.*, 2011). Because of niche breadth, generalists often have an easier time colonizing islands than specialists (e.g. Ebenhard, 1991). This pattern is seen in *Hyposmocoma*, where many species are generalist lichenovores, fungivores or generalist predators and few appear to be specialists (Rubinoff, 2008).

A study on *Anolis* lizards has revealed that unrelated lizards can fill similar empty niches on islands, often resulting in a stepwise and predictable sequence of ecomorph evolution (Losos, 1992). Our study reveals that living within rotting wood is the most plausible ancestral ecomorph for both purse case lineages. Ancestral

state reconstruction of *Hyposmocoma* reveals a fairly clear pattern of microhabitat use from tree bark (yellow, Fig. 2) to dead wood (red). Leaf litter, dry rock surfaces, wet rocks and exposed leaves appear to be derived ecomorphs, arising from tree bark or leaf litter ecomorphs. The sister subgenus, *Euperissus*, lack larval cases and feed internally on trees and shrubs or are external feeders of mosses growing on trees (Zimmerman, 1978; but see also Kawahara *et al.*, 2011b). Thus, it may be that the ancestor of *Hyposmocoma* + *Euperissus*, whose split is dated in the current study as approximately 18.4 Ma, fed internally on tree bark and this continued into *Hyposmocoma*, whereas it did not in *Euperissus*. Broad sampling and ecological data for many *Euperissus* species will be needed to test this hypothesis.

It is striking that both purse case groups appear to have invaded Oahu at the same time, suggesting that the presence of a member of one species group did not force the other to occupy a different niche when they co-occurred. Both case types may have shared habitats for millions of years, and this is plausible given the fact that purse cases do not appear to have strong preference for the type of wood they inhabit (Kawahara & Rubinoff, 2012).

Larvae of other *Hyposmocoma* typically prefer exposed surfaces and have more rough textured cases that may aid in camouflage (Zimmerman, 1978; Rubinoff & Schmitz, 2010). *Hyposmocoma* caterpillars are heavily attacked by explosive endemic radiations of parasitoid wasps in the families Bethyridae and Eupelmidae that are found on all Hawaiian islands, including the NWHI (Nishida, 2002). Although direct experiments confirming this assumption are yet to be performed, rearing dozens of larvae suggest that purse case species host considerably fewer parasitoids than other lineages in the genus, such as the burritos. We have recorded parasitoids from hundreds of larvae from 40 species of *Hyposmocoma* of which 28 (70%) are burrito cases, 4 (10%) are candy wrappers, and none are purses. Softer and more exposed case types appear to be derived in *Hyposmocoma*, and they are often more abundant at any site than purse cases. We predict that purse cases evolved as an adaptation to tunnelling through dead wood and gained a means of protection from parasitoids, and softer and more exposed case types counter parasitoids by sheer abundance. It would be a valuable contribution to further examine host preference and parasitism rates among endemic Hawaiian parasitoid lineages.

Purse cases, in part, appear to have originated as concealed wood-feeding larvae in the NWHI. These islands are now dry and barren of large trees due to habitat destruction and invasive species. Phylogenetic studies that incorporate ecological data for a large number of endemic taxa are becoming increasingly important as the Hawaiian native ecosystem is under great threat. Without additional efforts to identify and conserve

cryptic endemic species, large endemic radiations, like *Hypomocoma*, may disappear.

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Author contributions

Both authors developed concepts, designed the study, contributed specimens to the project and discussed results and commented on all stages of the paper. A.Y.K. conducted all phylogenetic and molecular analyses. D.R. supervised the project.

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Supporting information

Additional Supporting Information may be found in the online version of this article:

Table S1 Taxa sequenced for the present study along with UH log, extract, and GenBank accession numbers for three genes.

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